THE REACTIONS OF THE PLANKTONIC COPEPOD, CENTROPAGES TYPICUS, TO LIGHT AND GRAVITY [1]

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Introduction

Field investigations on the vertical distribution of the plankton carried out by many different workers in recent years have established the occurrence of a diurnal vertical migration for most species of the zoöplankton. Since most investigators agree in considering light as an important controlling factor, it seemed desirable, following the work of Esterly, Spooner, Clarke and others, to attempt to study the light responses of a single planktonic species under controlled laboratory conditions.

Centropages typicus is a neritic copepod, extremely abundant off Woods Hole at certain times of the year. Clarke (1933) states that the adults show a diurnal vertical migration correlated with changes in the submarine illumination. A few preliminary observations in the laboratory showed us that the adult females are very definitely affected by light. It was therefore decided to conduct experiments on the phototropic and geotropic responses of these animals. Our choice was fortunate in that it was possible to obtain the copepods quickly and easily off Woods Hole, and to keep them at a conveniently low temperature in the laboratory to ensure their healthy existence for at least a few days.

Phototropism: Experiments with Tubes Horizontal

In order to separate the phototropic from possible geotropic responses, it seemed advisable to test first the reactions of the copepods to light in a horizontal direction.

Methods

The experimental animals were obtained in Vineyard Sound by towing a scrim plankton net horizontally near the surface for about fifteen minutes. The animals, collected in the glass jar attached to

[1] Contribution No. 207 from the Woods Hole Oceanographic Institution.

the net, were poured into 3 liters of sea water and transported immediately to the laboratory. The adult female *Centropages typicus* were selected in diffuse daylight using a wide-mouthed pipette and a binocular microscope. Usually 20 healthy appearing copepods were placed in each of two glass tubes (13 × 2½″), each of which was sealed at one end with a glass plate. The open ends of the tubes were then sealed with similar glass plates, and the tubes arranged in constant temperature tanks maintained at 12° C. in the darkroom.

The two experimental tubes could be separated from each other by a distance of 21 feet. It was thus possible to obtain a wide range of light intensities for any one source, by varying the distance between the light source and the tubes. The intensities of the various inside frosted bulbs employed were as follows:[2]

Wattage	*Approximate Intensity at 1 foot*
15	13.5 foot-candles
25	25.0 "
40	43.0 "
60	75.0 "
100	150.0 "

It should be borne in mind that all the light intensities mentioned in the text are only approximate figures.

The lowest intensities used were obtained by means of neutral filters in the form of opal discs and white paper, the percentage absorptions of which were obtained by means of a photoelectric cell. Since several filters were used together at the very lowest intensities, corrections were made for diffusion and back-scattering.

Each experimental tube was marked off into quarter-lengths, and the distribution of the animals at any time, under any one condition of light, was expressed as the numbers in each section. At the very low light intensities, counting of the copepods was facilitated by lighting the tubes from behind for a moment with a weak red lamp. Preliminary tests made with this lamp showed that it had no effect on the distribution of the animals.[3]

In all the experiments, unless otherwise noted, the distribution of the animals was observed at the end of each time interval shown in the tables. After each observation, the tubes were changed, end for end, by turning them slowly in a horizontal plane. This procedure forced the animals to orientate afresh, and to redistribute themselves accord-

[2] On the advice of Mr. Eddie Kline, electrical engineer of the Canadian Laco Lamp Co., these can be considered as accurate only within 20 per cent, due to voltage fluctuation.

[3] Dr. Horton of the Department of Physics, McGill University, kindly made a spectroscopic photograph of the light emitted and found that the transmission begins at 6402 Å, and continues beyond 8600 Å.

ing to the tropistic responses actually in operation during that time interval. Enough time was allowed for the animals to establish their

TABLE I

Experiment commenced at 4:00 P.M., August 19.
Tubes *A* and *B* set at distance of 5 ft. and 1 ft. respectively, from source.
At 12:00 noon, August 20, tube *A* moved to 10 ft.
At 4:00 P.M., August 20, tube *A* moved to 20 ft.
Tube *B* was kept at 1 ft. throughout.
Source: 60-watt lamp.

Time	Distance	Intensity	(Positive) * I	II	III	(Negative) IV
Aug. 19						
4:10 P.M.	5 ft.	3.0 f.c.	20	–	–	–
	1 ft.	75.0 f.c.	20	–	–	–
4:40 P.M.	5 ft.		20	–	–	–
	1 ft.		20	–	–	–
6:45 P.M.	5 ft.		16 and 4	–	–	–
	1 ft.		20	–	–	–
9:15 P.M.	5 ft.		10 and 6	–	2	3
	1 ft.		10 and 3	3	–	1
9:30 P.M.	5 ft.		8 and 6	–	2	2
	1 ft.		3 and 7	3	3	2
Aug. 20						
11:30 P.M.	5 ft.		10 and 3	1	4	3
	1 ft.		4 and 8	3	1	1
2:30 P.M.	10 ft.	0.75 f.c.	8 and 3	–	3	3
	1 ft.	75.0 f.c.	5 and 9	3	1	1
4:00 P.M.	10 ft.		8 and 4	4	4	–
	1 ft.		3 and 7	4	1	1
4:45 P.M.	20 ft.	0.19 f.c.	9 and 6	–	3	–
	1 ft.	75.0 f.c.	5 and 10	3	2	1
8:00 P.M.	20 ft.		6 and 9	–	2	2
	1 ft.		3 and 9	4	1	2

* Two numbers are sometimes given under Section I (e.g. 16 and 4). This distinguishes those copepods right at the positive end (16), from those still in this section but apparently less strongly attracted.

new distribution before a second record was taken, so that their final position was unaffected by the configuration of the previous time interval.

Observations

A series of tests (Table I) was first carried out in order to determine:

(1) The normal responses of the copepods to various light intensities within limits found in nature.

(2) The effect of continued exposure to constant light intensities over the range studied.

The results obtained (Table I) showed that the copepods were positive to all illuminations, and remained largely so after exposure.

A number of experiments was then carried out to determine the range of light intensities to which the copepods were sensitive, and to investigate the possibility of the existence of critical light intensities at which the phototropic sign might become reversed.

The copepods were found to be positive to low light intensities, the lowest to which they were attracted being *ca.* 0.005 f.c. (Table II).

TABLE II

Responses to low light intensities. Distance of experimental tube from source: 20 ft. throughout.*

Intensity	Time	(Positive) I	II	III	(Negative) IV
0.06 f.c.	Aug. 20 9:30 P.M.	5 and 4	–	2	3
" "	Aug. 21 8:30 A.M.	4 and 6	1	2	1
0.015 "	10:45 A.M.	0 and 12	–	3	1
" "	12:00 Noon	2 and 12	1	2	3
" "	3:30 P.M.	4 and 5	1	4	–
0.008 "	Aug. 24 12:40 P.M.	14	1	3	2(New animals)
" "	2:00 P.M.	1 and 10	2	2	3
" "	3:00 P.M.	3 and 9	1	3	3
0.006 "	3:30 P.M.	11	2	1	3
" "	4:50 P.M.	6	5	–	7
" "	7:00 P.M.	11	2	2	1
" "	8:00 P.M.	10	–	2	7
" "	10:50 P.M.	13	–	4	1
" "	Aug. 25 8:30 A.M.	15	1	–	–
" "	9:30 A.M.	14	–	2	1
0.005 "	Aug. 26 12:30 P.M.	9	5	4	1
" "	1:55 P.M.	10	4	3	–
" "	2:25 P.M.	3	7	6	3
0.003 "	Aug. 28 2:30 P.M.	3	4	7	6(New animals)
" "	4:45 P.M.	9	4	4	3
" "	Aug. 29 9:40 A.M.	11	6	2	–
" "	11:50 A.M.	4	6	3	6
" "	6:45 P.M.	8	3	3	3

* Each time the light intensity was changed, it was done immediately following the preceding observation.

On continued exposure to the much higher light intensities of 150 and 600 f.c. (Table III), the majority of animals on the whole exhibited a positive phototropism, although at times there were more animals in the darker half of the tube and some of the animals apparently became negative on prolonged exposure.

It seemed desirable to determine whether the copepods would be repelled by the still higher light intensity (11,380 f.c.) approximating to that of bright sunlight. As a check on the results, other copepods which had been collected at the same time were subjected to a much lower intensity of 4 f.c. The results (Table IV) show that, at least after a short exposure to this very high intensity, half of the animals became negatively phototropic, while the others remained positive.

TABLE III

Responses to high light intensities
Source: 100-watt lamp. Intensity at ½ ft. : 600 f.c.
Intensity at 1 ft. : 150 f.c.

Time	Distance	(Positive) I	II	III	(Negative) IV
Aug. 30 5:00 P.M.	½ ft.	15	–	–	3
	1 ft.	14	–	2	3
5:30 P.M.	½ ft.	13	1	1	3
	1 ft.	13	–	1	6
6:45 P.M.	½ ft.	14	1	2	1
	1 ft.	10	1	–	8
9:00 P.M.	½ ft.	14	–	1	2
	1 ft.	14	1	2	3
10:15 P.M.	½ ft.	14	2	2	–
	1 ft.	10	–	1	8
Aug. 31 9:10 A.M.	½ ft.	5	1	2	10
	1 ft.	12	3	3	2
10:20 A.M.	½ ft.	8	1	3	7
	1 ft.	10	–	2	8
11:15 A.M.	½ ft.	11	2	1	4
	1 ft.	9	–	2	8
12:15 P.M.	½ ft.	9	1	1	8
	1 ft.	10	2	3	6
1:20 P.M.	½ ft.	12	2	–	4
	1 ft.	12	2	2	4
4:00 P.M.	½ ft.	12	2	–	4
	1 ft.	8	2	2	8
5:00 P.M.	½ ft.	12	1	3	3
	1 ft.	11	2	–	7

It was rarely that all the animals displayed an invariable reaction (either positive or negative) to any one condition of light. It was possible then that some of the animals were negatively phototropic even though the majority were positive; or again, perhaps some were indifferent. To gain evidence on these points, observations were made on individuals, one being sealed within a tube. At first, observations were made for the most part once every hour, using three widely separated intensities: 3.0, 150, and 600 f.c.

At the lowest intensity (3.0 f.c.), an individual remained photopositive for four hours, but appeared to become indifferent after exposure overnight. A second individual was indifferent from the first, and remained so for 15 hours. This behaviour was not modified if the individual was left in darkness, and then exposed to the light.

TABLE IV

Source: 1000-watt lamp. Tube at 4½ inches from source.
Control tube at 20 feet.
Ice added to aquarium to offset intense heat from source.

Time	Intensity	(Positive) I	II	III	(Negative) IV
11:40 A.M.	11,380 f.c.	10	–	2	6
	4 f.c.	8	4	1	6
11:55 A.M.	11,380 f.c.	12	–	–	6
	4 f.c.	11	2	–	5
12:05 P.M.	11,380 f.c.	8	1	–	9
12:20 P.M.	11,380 f.c.	10	–	4	6
	4 f.c.	13	–	2	3
1:20 P.M.	11,380 f.c.	8	1	2	10
	4 f.c.	11	2	2	3
1:35 P.M.	11,380 f.c.	9	1	3	8
1:45 P.M.	11,380 f.c.	8	1	3	8
	4 f.c.	15	2	2	–
2:00 P.M.	11,380 f.c.	9	–	–	9
2:10 P.M.	11,380 f.c.	10	1	1	7
	4 f.c.	14	2	1	1
2:25 P.M.	11,380 f.c.	11	1	–	7
2:40 P.M.	11,380 f.c.	8	1	–	11
	4 f.c.	14	2	1	1

The responses of two individuals at an intensity of 150 f.c., and of two others at 600 f.c. were such that one individual at each intensity remained positive for 24 hours, while the other individuals were positive for the first 5 hours but apparently became indifferent after exposure overnight.

More extensive experiments on individuals were carried out, making observations every ten minutes, so long as it was possible to do so, over a long period of time, and at a wide range of intensities (600, 150, 75, 67, 33, 13.5, 2.4, 0.87, 0.03, 0.006, and 0.002 f.c.). Of four individuals (*A*, *B*, *X*, and *Y*), specimens *B* and *Y* were strongly and constantly photopositive to all the above intensities; indeed, specimen *B* was never recorded outside Section I. Individual *A* was in the main attracted although less so at intensities above 75 f.c. Individual *X*, although less consistent, was generally attracted by the light, but occasionally at both high and low intensities it was found at the negative end of the tube, even from the beginning of the experiment.

Having studied the effects of continued exposure to different intensities, it was decided to determine the effect of changing light intensity—a condition which is more like that which occurs in nature. The changes in intensity were obtained by varying the position of the source relative to the two experimental tubes. Thus the quality of the light remained unchanged, and two experiments could be carried on at once.

Successive experiments were carried out by moving the source first 1 foot, then 2, 5, 10, and finally 20 feet every ten minutes (owing to difficulties in counting, 15-minute intervals were sometimes unavoidable). The intensities ranged from 11,380 to 4 f.c. Before the experiments were commenced, the tube at the maximum intensity was left exposed to light until a considerable percentage of the animals exhibited repulsion.

Regarding the one-foot changes: On increasing the intensity from 4 to 11,380 f.c., the animals remained continually attracted showing always at least 80 per cent in the positive half of the tube. However, after continued exposure for one hour at the highest intensity, only 40 per cent were still attracted. In the opposite tube, 55 per cent of the copepods were repelled at the beginning when the intensity was 11,380 f.c., and it was necessary to decrease the intensity to 64 f.c. before 80 per cent of the animals were attracted.

Considering the results of the 2 ft. changes, it was found that essentially similar conclusions could be reached. In the increasing intensity experiment, actually 100 per cent of the animals exhibited constant positive phototropism. Decreasing the intensity resulted in progressive attraction down to 16 f.c., when about 80 per cent of the animals were in Sections I and II. Further decreases caused little change.

The 5, 10 and 20-foot changes may be considered together. Regarding the increasing intensities, it is striking that none of the changes had any effect on altering the original distribution of the animals. The numbers of animals in each half of each tube remained almost perfectly constant with the ten-minute intervals allowed, and it was only after prolonged exposure (45 to 60 minutes) at 11,380 f.c. that repulsion was brought about. Of the decreasing intensity experiments, in the 5-ft. changes progressive attraction resulted in 80 per cent of the animals being positive at an intensity of 7 f.c. Progressive attraction also resulted in the other experiments, with 70 per cent of the animals being attracted in the 10-ft. changes at the minimum intensity of 4 f.c. (After one hour at 4 f.c., 80 per cent were positive.)

All these experiments on different magnitudes of decrease, each occurring with 10-minute intervals, would seem to indicate that the greater the magnitude of change, the lower the intensity at which a large number of the copepods became positively phototropic. This statement may be misinterpreted unless it be remembered that undoubtedly 80 per cent, or more, of the copepods would have migrated to the positive half of the tube at much higher intensities had more time been allowed before the next change was made. (There would thus appear to be a "time-lag" effect.)

The above experiments show the effects of different magnitudes of increase and decrease with a constant time interval of 10 minutes. The percentage relationship between any one intensity and that which immediately preceded it is not by any means constant during any one succession of changes. Thus experiments were next conducted similar to the foregoing, except that there was a constant percentage increase or decrease throughout each series of changes. The actual rates of change used were such as may occur in nature. (The values chosen were the maximal changes observed by Clarke (1933) at one station in the Gulf of Maine.)

Increases and decreases of 10 per cent per hour were first tried, through a range of high intensities (11,380 to 2,840 f.c.), and then through a low intensity range (9.5 to 6.2 f.c.). Considering first the decreasing intensities, through the high range there was progressive attraction, while through the low range there was practically no alteration in the distribution. As regards the increasing intensities experiment, there was little observable change, but, if anything, a rather larger percentage of animals was attracted with time. The same result was obtained with the low intensity range. Decreases and increases of 20 per cent per hour, through both high and low intensity ranges, gave similar results.

Phototropism and Geotropism: Experiments with Tubes Vertical

Parker, Dice, Esterly, Clarke and others have demonstrated that geotropism is frequently an important factor in the vertical migration of plankton. It seemed desirable, therefore, to carry out experiments using vertical tubes to ascertain whether the light responses would be different, and to test for the occurrence of a true geotropic reaction.

Methods

The aquaria were replaced by two large bell-jars held upright by specially constructed wooden stands. The same experimental tubes were used, but they stood vertically in all the following experiments. A lamp was suspended over each tube, and, by means of a pulley system, the distance between the lamp and the tube could be quickly altered. The maximum distance thus obtainable was $4\frac{1}{2}$ feet. Whenever it was desired to illuminate the animals from below, the tubes were simply placed upright on an iron tripod, and the lamp placed underneath.

Observations

It was decided to find the effects of various rates of change of light intensity, and to compare the results with those obtained in the horizontal experiments. Unfortunately the 1,000-watt lamp burned out and as it was impossible to replace it in the short time remaining, it was necessary to confine the indoor experiments to the lower light intensities (0.67 to 240 f.c.). A wide variety of rates of change was used: 25 per cent per hour, and 25, 50, 100, 300, and 700 per cent per half-hour.

Considering the experiments on increasing light intensities the following conclusions were reached. Within the range of intensities used, it seemed that, in general, increasing the light at a variety of rates does not bring about repulsion. One experiment, however, using 25 per cent increases per half-hour, through a range from 7.4 to 19.1 f.c. did cause repulsion:—70 per cent of the copepods were attracted initially, but as the intensity increased, fewer remained positive until only 16 per cent were attracted at 19.1 f.c. A large number of other experiments, however, at intensities near 7.4 to 19.1 f.c. (also at higher and lower ranges, and at rates from 10 per cent to several hundred per cent) was carried out, and in no other case was this repulsion observed. In the great majority of cases the distribution remained almost constant. It may be then, that this single case of repulsion does not demonstrate the normal behaviour of these animals, at least under laboratory conditions.

In the experiments on decreasing light intensities, with the exception of a single experiment, decrease in intensity at all rates, and through all the ranges of intensity employed, resulted in more and more of the animals swimming to the top of the tube as the light diminished.

This progressive attraction was sometimes very great. For example, in two experiments only 25 per cent of the copepods were positive at the beginning, and nearly 90 per cent at the end. The exceptional experiment was the only one employing so low a rate of decrease as 10 per cent. It is possible that such changes are too slow to be perceptible to the animals (below threshold).

It was thought desirable to determine the effect of increasing light intensity, using direct sunlight, so that a very high intensity range would be available. The experiment was conducted in the open behind the Oceanographic Institution. An inverted bell-jar was used as in the darkroom, with the experimental tube placed inside it, standing vertically. Since it was here impossible to circulate cooled water through the bell-jar, it was simply refilled with cold sea water whenever the temperature rose. The stand holding the bell-jar was completely

TABLE V

Reactions to direct sunlight

Time	No. of Opals	Relative Sunlight	Approximate Int. in Tube (f.c.)	(Top) I	II	III	(Bottom) IV
		per cent					
12 Noon	4	100	1,080				
12:30 P.M.	4	100	1,080	11	1	4	3
1:00 P.M.	3	98	1,400	11	1	3	3
1:30 P.M.	2	93.6	2,000	12	1	1	4
2:00 P.M.	1	88	2,640	19	–	–	1
2:30 P.M.	0	79	9,470	11	2	1	5
3:00 P.M.	0	73	8,760	11	–	1	5
3:30 P.M.	4	59	636	12	–	3	3
4:00 P.M.	2	43.6	935	5	2	6	4
4:45 P.M.	0	27	3,240	7	1	3	7

covered with black tar-paper. A small aperture cut in the top allowed a beam of sunlight to fall on the top of the experimental tube. On one side of the stand, the tar-paper formed a moveable flap which could be lifted, and the necessary counts made. Four opal diffusing discs were placed over the aperture to reduce the light; these were removed at intervals. In the first experiment, they were removed one at a time, in the second two at a time, and in the last experiment all four were removed together. Each disc alone transmits 25 per cent of the light falling upon it. The beam of sunlight was directed on to the aperture above the tube by means of a simple plane mirror which could be turned as the sun changed its elevation. The light intensity was measured by means of a Weston Photronic Cell.

The results of the experiment (Table V) show that when the light had increased from about 1,000 to about 9,000 f.c. over a period of two hours, the animals were at all times strongly photopositive. However, increases starting at lower intensities resulted in a majority of the animals in the lower half of each tube. Is there also a negative geotropism which becomes stronger with increase in light intensity? Certainly the results indicate that mere rate and direction of change of light alone cannot account completely for the movements of *Centropages typicus*.

Thus experiments were next carried out in order to test the possibility that the copepods might react to gravity, and that the above results were only partially due to phototropic responses.

The experimental tubes were placed vertically in the bell-jars in the normal way. The animals were then left in darkness, and counts made later with the red lamp. For example, the tubes were left for $1\frac{1}{2}$ hours in darkness and subsequent counts gave the following results (Tubes *A* and *B* were treated identically to furnish checks on each other):

	(Top) I	II	III	(Bottom) IV
Tube *A*	14	4	1	–
Tube *B*	6	4	–	8

The tubes were then reversed vertically end for end. After one-half hour the following results were obtained:

	(Top) I	II	III	(Bottom) IV
Tube *A*	12	5	3	–
Tube *B*	12	3	–	3

The tubes were again reversed. After one-half hour the following results were obtained:

	(Top) I	II	III	(Bottom) IV
Tube *A*	11	3	1	2
Tube *B*	15	1	–	3

The above results clearly show that the animals are on the whole negatively geotropic in darkness. Careful observation showed that the animals sink rapidly if they cease swimming. Hence actual effort was necessary for them to remain at the tops of the tubes, and the geotropism must then be quite strong.

The relation between geotropism and phototropism was then tested by taking the above animals from darkness and illuminating them from below, with the following results:

	(Top) I	II	III	(Bottom) IV
Tube *A* (15-watt lamp below)	7	4	3	4
Tube *B* (100-watt lamp below)	–	1	–	19

The results would indicate that negative geotropism is stronger than positive phototropism when the light is weak, while positive phototropism is overwhelmingly strong when the intensity is high.

Tube *B* was returned to darkness and a count 15 minutes later showed that the majority of animals were in Section I.

These results verified the negative geotropism. A 60-watt lamp was then placed below the tubes and the following results obtained:

	(Top) I	II	III	(Bottom) IV
Tube *B* (60-watt lamp below the tube)......	1	–	–	19

Both tubes were again returned to darkness and a count 45 minutes later again showed a large majority exhibiting negative geotropism. A 25-watt lamp was then placed below the tubes:

	(Top) I	II	III	(Bottom) IV
Tube *B* (25-watt lamp below the tube)......	4	1	3	9

The experiment was repeated. The animals again showed negative geotropism in darkness. With a 25-watt lamp below the tubes the results were as follows:

	(Top) I	II	III	(Bottom) IV
Tube *B* (25-watt lamp below the tube)......	4	1	–	12

Finally it was decided to determine the effect of replacing a low light intensity by a high one, when the geotropism and phototropism were in opposition. It has been shown that after exhibiting negative geotropism in darkness, on exposure to a 25-watt bulb from below the distribution was:

	(Top) I	II	III	(Bottom) IV
Tube *B* (25-watt lamp below)..............	4	1	–	12

This lamp was then replaced by a 100-watt lamp. A count after 15 minutes showed:

	(Top) I	II	III	(Bottom) IV
Tube *B* (100-watt lamp below).............	–	–	–	17

All the above experiments definitely establish that the adult female *Centropages* is primarily negatively geotropic and positively phototropic. When the two are acting in opposition, the positive phototropism becomes progressively stronger as the light intensity increases.

Discussion

It is still a controversial matter how far laboratory experiments of the type conducted are applicable to conditions in nature. Throughout all the experiments, however, it was our aim to avoid "shock" conditions, and the use of surface tow-nettings avoided large changes in light intensity during the collections.

It would seem from the experiments with artificial light, that adult female *Centropages typicus* should be right at the surface during most of the day, since they are strongly positively phototropic to a very wide range of light intensities, and it does not seem that continual decreases are always necessary to cause a majority to remain positive, such as was found to be the case with *Acartia clausi* (Johnson, 1938). However, repulsion does occur to some extent on prolonged exposure to very high intensities, and also in the experiments using direct sunlight (Table V) when the illumination increased through such ranges of low intensities as may occur in the early morning. Hence, after considerable exposure to strong sunlight (about midday in summer) and possibly also when the light is increasing in the early morning, *Centropages* might be expected to be a little lower in the water.

G. L. Clarke (1933) however, found that these copepods have a maximum of about 13 m. during most of the day in the Gulf of Maine. Some hauls made in August, 1935, near Woods Hole, were examined and these in general confirmed this finding, although there were cases when the majority were at the surface. (Clarke also did find, for two stations, the majority at the surface.)

In considering this difference it must be remembered that there are other factors acting in nature. Thus, especially at the surface, turbulence may carry the copepods to somewhat lower depths. Further, the possibility of muscular fatigue must not be overlooked. As has been mentioned, *Centropages* will sink rapidly as soon as it ceases swimming, and thus some will tend to sink below the surface, though positively phototropic. This probably accounts for the observation, that, although using the same intensities, a considerably larger percentage of animals is found in the negative half of the tube in the vertical experiments than in the horizontal ones. It should also be noticed that Clarke did find a secondary maximum of *Centropages* at the surface.

The rise to the surface at night, observed by Clarke and others, is explainable since *Centropages* is always very strongly attracted when the light intensity is diminished. The negative geotropism, evident at least during and just after exposure to darkness, will aid the rise.

Parker (1901) found that female *Labidocera* migrate surfacewards at night due to positive phototropism and negative geotropism, and Dice (1914) considered geotropism the major factor in the migration of *Daphnia*. However, the recent findings of Kikuchi (1938) exemplify the fact that the actual rôle played by geotropism probably varies from species to species.

Since *Centropages* is positively phototropic to very low intensities, the upward migration will presumably continue when the light is exceedingly weak. Further, when the animals have reached the surface, they will tend to remain there during darkness owing to the negative geotropism, and they will not take up a more or less uniform distribution, as Russell has supposed for some planktonic species.

As regards the downward migration in the morning, we were generally unable to demonstrate repulsion with increase in light intensity using electric light in the laboratory. However, in the experiments using direct sunlight, it was shown that increase in intensity at a low intensity range from about 700 to 3,500 f.c., did cause repulsion, and this range of light change might be expected in the early morning. It is possible that exposure to darkness during the night might also tend to render the animals more sensitive to light, but there is the opposing geotropism to consider. This has been shown, however, to be definitely weaker for average light intensities. Further experiments, however, are desirable in this connection.

Although no experiments were conducted to test specifically Esterly's theory of a diurnal rhythm (Esterly, 1917, 1919), it would seem from an examination of our readings at different times of the day that such a rhythm is absent in *Centropages*. Rose considers that a species exhibiting diurnal vertical migration is adapted to a certain optimum light intensity (Rose, 1925). Many investigators have been unable to demonstrate such optima in the laboratory. Esterly, for example, found *Calanus* negative to all intensities used, provided the temperature was above 10° C. Rose believed that if a wide range of intensities was employed in the experiments, the optima would be demonstrable. We therefore used a very wide range in our experiments, but did not find any such optimum for *Centropages*.

Reversal of phototropic signs with absolute intensity of light was also difficult to obtain, though Loeb, Parker, Rose, etc. have demonstrated this for many planktonic species. It should be noted that Clarke also found there was no evidence from his experiments for an optimum light intensity in *Daphnia*. He also found that reversal of phototropic sign could not be brought about by absolute light intensity in this form. (Clarke, 1930 and 1932.)

Various authors have frequently pointed out the complexity of the problem of vertical migration by showing differences in behaviour between different species (e.g. Clarke, 1933), between the sexes of a single species (e.g. Russell, 1928), and between ages of the same sex of one species (e.g. Gardiner, 1933). The observations of the authors of the present paper further illustrate that although the majority of adult female *Centropages typicus* do behave in a similar manner, variation in vertical distribution between individuals may be expected even when they are of the same species, sex and age. This is in agreement with field studies.

Summary

Experiments on phototropism and geotropism in adult female *Centropages typicus* were conducted. The following conclusions were indicated:

A. Experiments with experimental tube horizontal.

1. The copepods are primarily photopositive and constant exposure does not modify this reaction except at very high intensities in the neighborhood of that of bright sunlight (*ca.* 12,000 foot-candles) when a large number exhibited negative phototropism after continual exposure for about an hour.

2. The lowest intensity at which there were always more copepods in the brighter than the darker half of the tube was *ca.* 0.005 f.c.

3. There are two types of individuals. One type, after continuous exposure to light, becomes indifferent. In the other type, the animals are persistently attracted.

4. Decrease in light intensity, at a variety of rates and at a wide range of intensities, always results in increased attraction.

5. Increase in light intensity, at a variety of rates and at a wide range of intensities, has no effect on the behaviour. Only prolonged exposure at high intensities repels the animals.

B. Experiments with experimental tube vertical.

1. With the light from above the animals stay mainly at the top of the tube through a wide range of intensities, a distribution which is probably the result of positive phototropism, negative geotropism, or both.

2. Increases in intensity have no effect on the animals except when sunlight is used. A fair percentage of the animals is then repelled.

3. With the exception of decreases as low as 10 per cent per hour, decreases in intensity result in increased attraction.

4. The animals are strongly negatively geotropic in darkness. When geotropism and phototropism are opposed, the reactions depend upon the intensity of the light.

5. The possible bearing of these conclusions on the vertical distribution and diurnal vertical migration of adult female *Centropages typicus* is discussed.

BIBLIOGRAPHY

Clarke, G. L., 1930. Change of phototropic and geotropic signs in Daphnia induced by changes of light intensity. *Jour. Exper. Biol.*, **7**: 109–131.

——, —. —., 1932. Quantitative aspects of the change of phototropic sign in Daphnia. *Jour. Exper. Biol.*, 9: 180–211.

Clarke, G. L., 1933. Diurnal migrations of plankton in the Gulf of Maine and its correlation with changes in submarine irradiation. *Biol. Bull.*, **65**: 402–436.

Dice, L. R., 1914. The factors determining the vertical movements of Daphnia. *Jour. Animal Behavior*, **4**: 229–265.

Esterly, C. O., 1917. The occurrence of a rhythm in the geotropism of two species of plankton copepods when certain recurring external conditions are absent. *Univ. Calif. Publ. Zool.*, **16**: 393–400.

——, —. —., 1919. Reactions of various plankton animals with reference to their diurnal migrations. *Univ. Calif. Publ. Zool.*, **19**: 1–83.

Gardiner, A. C., 1932. Vertical distribution in Calanus finmarchicus. *Jour. Mar. Biol. Ass'n., N.S.*, **18**: 575–628.

Johnson, W. H., 1938. The effect of light on the vertical movements of Acartia clausi (Giesbrecht). *Biol. Bull.*, **75**: 106–118.

Kikuchi, K., 1938. Studies on the vertical distribution of the plankton Crustacea. *Records of Oceanogr. Works in Japan*, **10**: 17–41.

Loeb, J., 1908. Über Heliotropismus und die periodischen Tiefenbewegungen pelagischer Tiere. *Biol. Zentral.*, **28**: 732–736.

Parker, G. H., 1901. The reactions of copepods to various stimuli and the bearing of this on daily depth-migrations. *Bull. U.S. Bur. Fish.*, **21**: 103–123.

Russell, F. S., 1928. The vertical distribution of marine macroplankton. VII. Observations on the behavior of Calanus finmarchicus. *Jour. Mar. Biol. Ass'n., N.S.*, **15**: 429–454.

Rose, M., 1925. Contribution à l'étude de la biologie du plankton. Le problème des migrations verticales journalières. *Arch. de Zool. expér. et gén.*, **64**: 387–542.